

Condition dependence in the marine exit timing of sockeye salmon (*Oncorhynchus nerka*) returning to Copper Creek, Haida Gwaii

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Abstract: We examined a small population of sockeye salmon (*Oncorhynchus nerka*) that enters their natal stream, to hold in their natal lake, months (>130 days) prior to spawning. This effectively decouples the influence of spawn timing requirements and behaviours from river entry (alternately referred to as “marine exit”) timing and is therefore a good model to study the migration strategies specifically associated with marine exit. We found individuals with early marine exit had higher growth rates in the months prior to river entry, had greater lipid density, were more likely male, more likely of the 2.2 versus 1.2 age class, had smaller gonads, and (if female) had more and smaller eggs. Body size at river entry did not vary seasonally. These patterns are explained using a life history model proposing that individual fish exit the sea when the marginal fitness benefits of further growth are outweighed by the marginal fitness cost of further marine residence. This point is reached at different times depending on body size, sex, lipid reserves, and the growth rate.

Résumé : Nous avons examiné une petite population de saumons quinnats (*Oncorhynchus nerka*) entrant dans leur cours d'eau natal afin de demeurer dans leur lac natal, plusieurs mois (>130 jours) avant le frai. Cette approche dissocie dans les faits l'influence des exigences et comportements associés au moment du frai du moment de l'entrée dans la rivière (aussi appelée « sortie de la mer ») et constitue donc un bon modèle pour étudier les stratégies de migration spécifiquement associées à la sortie de la mer. Nous avons constaté que les individus dont la sortie de la mer est hâtive présentaient des taux de croissance plus élevés dans les mois précédant l'entrée dans la rivière et une plus grande densité de lipides, étaient plus susceptibles d'être des mâles et d'appartenir à la classe de 2,2 ans d'âge qu'à la classe de 1,2 an, avaient des gonades plus petites et (pour les femelles) avaient plus d'œufs, mais ces derniers étaient plus petits. La taille du corps au moment de l'entrée en rivière ne variait pas selon la saison. Ces motifs s'expliquent par un modèle de cycle biologique qui postule que les individus sortent de la mer quand les avantages marginaux pour l'aptitude de la poursuite de la croissance sont supplantés par le coût marginal pour l'aptitude de la poursuite de la résidence en mer. Le moment où ce point est atteint dépend de la taille du corps, du sexe, des réserves de lipides et du taux de croissance. [Traduit par la Rédaction]

Introduction

In anadromous fish, the time at which individuals leave the ocean and enter freshwater (“river entry” or “marine exit”) prior to spawning is an important life history event, and has been studied in terms of both mechanisms and fitness costs and benefits. In mechanistic terms, homeward migration from the open ocean by Pacific salmon species may be initiated by a population-specific “physiological switch”, regulated by photoperiod, and unaffected by location at sea (Gilhousen 1960; Quinn 1982; Hodgson et al. 2006). This mechanistic model suggests that intra-population variation in river entry date results from the oceanic distribution of individuals at the moment that homeward migration is initiated. Individuals closer to home arrive earlier than those further away. This displacement model has been used to explain interannual variation in river entry of Fraser and Bristol Bay sockeye salmon (*Oncorhynchus nerka*), the variation being attributed to the differing latitudinal distribution of fish in the North Pacific during warm versus cold winters (Gilhousen 1960; Blackburn 1987; Hodgson et al. 2006).

The timing of river entry of individuals can also be assessed as an evolved trait. Adult migration timing is known to be heritable (Hansen and Jonsson 1991; Smoker et al. 1998; Quinn et al. 2000), so natural selection can act on this trait (Quinn and Adams 1996). The presumption is that variation in the underlying physiological mechanism that triggers river entry leads to variation in survival or reproduction that can be acted upon by natural selection. Furthermore, this mechanism may be flexible and able to advance or delay the date of river entry in relation to factors such as size, growth rate, sex, and condition.

Energetic and reproductive state are important correlates of river entry timing within some Fraser sockeye salmon populations (Young et al. 2006; Cooke et al. 2008; Crossin et al. 2009), suggesting that physiological and behavioural mechanisms may enable fine-tuning of these broad patterns, for example deferring maturation when growth is poor (Parker and Larkin 1959; Bilton et al. 1982; Peterman 1985). River entry marks the end of the at-sea growth period, and is the first stage leading to spawning. “Age at maturity” life history models (Stearns 1992) provide a framework

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to study the point at which an organism ceases resource accumulation and switches to expending those resources on reproduction. These models can be applied to understand river entry decisions in sockeye and other Pacific salmon (Lewis 1987; Quinn 2005). The models suggest that the river entry decision is influenced by: (i) the growth rate at sea; (ii) the mortality rate at sea; and (iii) the energetic and mortality costs of upriver migration. The fitness benefit of prolonging ocean residence, for individuals that have experienced poor growth, is that body size and energy reserves can be increased, which may improve migratory capacity, competitive spawning ability, and fecundity (van den Berghe and Gross 1984; Fleming and Gross 1994; Gross 1985). However, these reproductive benefits can create extra exposure to mortality, setting up a trade-off. Finally, factors such as river flow (Kuparinen and Merilä 2009), temperature (Hodgson and Quinn 2002), or food availability at sea (e.g., Brodeur et al. 1996) may introduce additional explicit timing considerations if they vary seasonally and affect the cost of upriver migration or freshwater residence prior to spawning (Katinić et al. 2015).

The fitness-maximizing river entry date is reached when the fitness benefit of another day's ocean residence (reproductive increment) is offset by the fitness cost (survival decrement). If the benefit or the cost (or both) of extending ocean residence varies with size, age, growth rate, or energy reserves, the fitness-maximizing river entry date will be condition dependent, and will differ between individuals. This hypothesis predicts large and fast-growing individuals with high energy reserves will choose an earlier river entry date because the marginal benefits derived from remaining at sea are less than those gained by smaller and slower growing individuals with low energy reserves.

Previous work has examined condition dependence in the timing of entry to spawning areas of salmon in relation competitive spawning tactics. For example, Morbey (2000) explained protandry (males enter spawning areas sooner than females) by the mate opportunity hypothesis. Morbey and Ydenberg (2003) found that early- and late-entry females varied the allocation of resources to eggs and to somatic reserve in ways that they interpreted in relation to tactics related to female–female competition for nest sites.

Here, we investigate the condition dependence of river entry timing in the population of sockeye salmon returning to Copper Creek on Haida Gwaii, British Columbia (Katinić et al. 2015). This population has one of the longest known delays (>130 days) between river entry and spawning (cf. Hodgson and Quinn 2002), and Katinić et al. (2015) found no relation between the timing of river entry and the timing of spawning. Hence, this population appears well-suited to study the effect of condition on river entry timing independent of its influence on spawning tactics.

Methods

Study area

Copper Creek (53°9'29.98"N, 131°47'59.89"W) is located on Moresby Island in the Haida Gwaii archipelago, British Columbia. Sockeye salmon exit the ocean and migrate up Copper Creek into Skidegate Lake during May and June of each year (Katinić et al. 2015). Spawning occurs in several small creeks draining into Skidegate Lake during September and October. The period between river entry and spawning ranges from 83 to 163 days (Katinić et al. 2015) for individual fish.

Field procedures

Sockeye salmon were trapped in a weir located at the mouth of Copper Creek. The weir was run from 2 May to 26 June 2005, and 24 April to 29 June 2006. Meristics (sex, fork length \pm 0.5 cm) and scales (one from each side of the body) for age and growth analysis were collected from 317 fish in 2005 and 442 fish in 2006. Fish were removed from the trap using a cradle, placed into a foam-covered trough with flowing water pumped directly from the

stream, processed, and released upstream of the weir. Fish were inspected visually and assigned a sex based on external characteristics. Reliability of sex assignments based on external characteristics was validated with dissections. Sex was “unassigned” if external characteristics did not clearly demonstrate sex.

An additional random sample of 123 (2005) and 97 (2006) fish were harvested and dissected. These were sex-assigned based on gonad inspection; measured for fork length and post-orbital hypural length (\pm 0.1 cm) and body mass (\pm 0.1 g); and five scales were collected for age and growth analysis. Gonads were removed and the head cut off approximately 2.5 cm behind the distal edge of the operculum. The wet mass of gonads and heads was determined using a digital field scale (\pm 0.1 g). The carcass and gonads were placed in airtight bags, transported to the laboratory, and stored at -20 °C.

Age and growth

Acetate impressions of the scales were made using a hydraulic press and visually interpreted by Birkenhead Scale Analysis (Lone Butte, British Columbia) to determine age, using the standard method of the Pacific Salmon Commission, based on that described by Clutter and Whitesel (1956), and Gamble and Cox-Rogers (1993). Circuli counts and distances between annuli were measured on a 20° alignment of the ventro-anterior axis using a projection microscope at \times 100 magnification and a Calcomp digitizer. Number of circuli and distances between annuli were used to estimate growth rates. Fork lengths at the first and second annulus and the scale edge for each fish was estimated using Fraser-Lee's formula as suggested by Ricker (1992). Scales exhibiting resorption up to last marine annulus, where the spring growth following last annulus was not visible, were removed from the analysis. Increases between circuli spacing are associated with increased food availability (Barber and Walker 1988) and are commonly observed to start the next year of growth after the winter annulus during March (Carol Lidstone, Birkenhead Scale Analysis, personal communication, 2005).

Fish age is reported following Koo (1962), in which the notation “1.2” refers to fish that have spent 1 year in freshwater (fry to smolt) and 2 years at sea (smolt to adult), and “2.2” refers to fish that have spent 2 years in freshwater and 2 years at sea. Specific growth rate ($\text{mm}_{(\text{growth})} \cdot \text{mm}_{(\text{length})}^{-1} \cdot \text{day}^{-1}$) was estimated as the difference in back-calculated fork length between the beginning and end of a period (growth), divided by fork length at the end of that period and then divided by the duration of the period. Growth rates at sea were estimated for the first and second years (years arbitrarily defined to end 31 March), and for the spring prior to river entry. Specific growth rate during the spring prior to river entry is estimated as the difference between the fork length at capture and the back-calculated fork length at the end of the second annulus, divided by the fork length at capture and then divided by the number of days between 31 March and the date of capture.

Gonad size and fecundity

The gonads were thawed and reweighed (\pm 0.1 g) to account for dehydration associated with freezing. Total dry gonad mass was estimated by drying a subsample of tissue at 95 °C for 24 h. Individual egg mass was estimated from the mean wet and dry masses of 10 eggs. Fecundity was estimated by dividing the mass of the whole ovary by the mass of a subsample with a known number (\sim 100) of eggs.

Energy density

Each carcass was thawed and reweighed (\pm 0.1 g) to account for dehydration associated with freezing. A \sim 2 cm cross section of the body was cut posterior to the head and gill cover, weighed (\pm 0.1 g), homogenized (Cuisinart Mini-Prep Plus Processor), and a 25 g sample collected for tissue analysis. Lipid, water, and carbon contents (%)

Table 1. Mean trait values of sockeye salmon entering the Copper River, Haida Gwaii, in 2005 and 2006.

Trait	2005	2006	% difference
Weir operated	2 May – 26 June	24 April – 29 June	—
No. of fish entering	4065	11 920	—
Median date of entry	26 May	22 May	—
No. trapped and released	317	442	—
No. trapped and sacrificed	123	97	—
Total	440	539	—
Overall body mass (g)	1622.4	1638.7	+1.0
SD of mean body mass (g)	293.3	249.9	—
Proportion females	0.56	0.57	—
Fork length males (mm)	518±5 (128)	509±5 (200)	-1.8
Fork length females (mm)	512±5 (163)	503±3 (288)	-1.8
Body mass males (g)	1670.8±79.6 (49)	1626.1±96.8 (27)	-2.7
Body mass females (g)	1582.9±76.7 (60)	1648.5±81.1 (35)	+4.0
Proportion aged 1.2	0.65	0.63	—
Fork length 1.2 (mm)	515±6 (202)	502±3 (305)	-2.6
Fork length 2.2 (mm)	515±6 (89)	512±4 (177)	-0.6
Body mass 1.2 (g)	1575.8±74.9 (66)	1645.9±71.5 (42)	+4.3
Body mass 2.2 (g)	1693.9±77.9 (43)	1643.0±123.4 (22)	-3.1

Note: Values are reported (where applicable) as mean ± 95% confidence interval (n). “% difference” is calculated as (2006 value – 2005 value)/(2006 value).

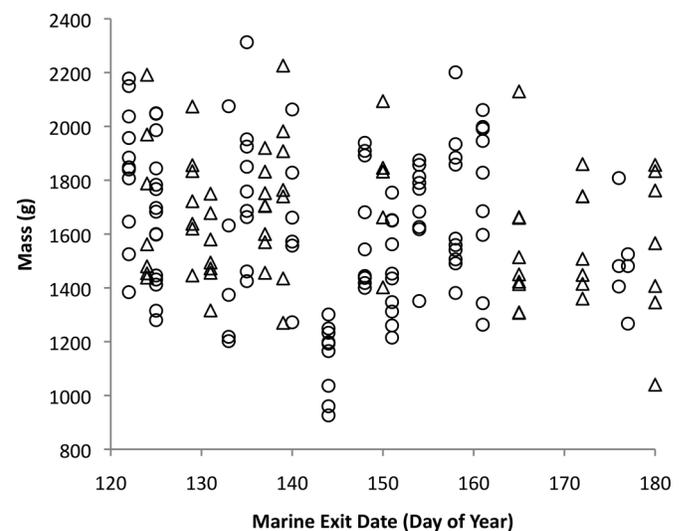
were determined according to methods outlined by Higgs et al. (1979). Briefly, lipid content was determined using an extraction of 2 g wet mass of homogenized tissue in 40 mL of solvent, 1:1 chloroform–methanol, and 8 mL of distilled water, follow by a secondary solvent wash. Water content was determined by the difference in mass of a sample of homogenized tissue dried at 95 °C for 24 h. Carbon was determined by the mass of ash remaining from the sample of dried homogenized tissue after combustion at 600 °C for 2 h. Protein was estimated as the difference between 100 and the summed percentages of lipid, water, and carbon, as in previous studies (Berg et al. 1998; Hendry and Berg 1999; Hendry et al. 1999; Crossin et al. 2004). The lipid and protein contents were multiplied by 0.03954 MJ·kg⁻¹ and 0.02364 MJ·kg⁻¹, respectively, to estimate their energetic equivalents, and summed to estimate the total energy content of each fish (Higgs et al. 1979).

We validated the cross section method by combining the remainder of the cross section with the original carcass and viscera, minus the gonads (n = 18), homogenizing in an industrial food processor (Robot Coupe Blixer BX6V), and withdrawing a 25 g sample for comparison with the cross-section sample.

Data analysis

JMP 7.0.2 (SAS Institute Inc.) was used for statistical analyses. Comparisons of means were tested using one-way ANOVA with Tukey–Kramer tests or a two- or three-factor general linear model (GLM) when testing with age and (or) sex as covariates. Homogeneity of variance was tested using O’Brien’s test. In cases where violations of homogeneity of variance were detected, the Welch ANOVA for the means was used. Least squares regression analysis was used to test significance of correlations of body size, growth rate, energy density, fecundity (egg number), and gonad size versus river entry date with age and (or) sex as covariates. Significance levels were Bonferroni-adjusted for sets of similar comparisons. For example, growth rate and river entry were compared in four tests (growth rate in 2005 and 2006 for both the first and second years at sea), so the significance level was α/4. A general linear model with interaction terms was used to verify that tissue subsamples (dorsal cross section) represent the whole carcass for energy density analysis of somatic tissue. The assumption of normality for linear regression was tested using the Shapiro–Wilk test. In cases where data failed the Shapiro–Wilk test, data were log transformed prior to statistical testing.

Fig. 1. Body mass by marine exit day for fish returning in 2005 (circles: n = 109, p = 0.125) and 2006 (triangles: n = 64, p = 0.056).



Results

A total of 4065 sockeye salmon entered the Copper River in 2005, and 11 920 in 2006. The median date of river entry was 26 May in 2005, and 22 May in 2006. Characteristics of the sockeye populations entering in the 2 years are compared in Table 1.

Differences in mean body mass and mean fork length between sex and age classes are small both within and between years. While there was considerable within-year variation, there were no statistical differences in body size detected between years (mass ± SD, 2005: 1622.4 ± 293.3 g; 2006: 1638.7 ± 249.9 g) (Fig. 1). Neither fork length (2005: n = 399, p = 0.368; 2006: n = 491, p = 0.914) nor body mass (2005: n = 109, p = 0.125; 2006: n = 65, p = 0.056) changed significantly over the course of the river entry period within either year.

Other traits did change consistently with river entry date. The overall sex ratio (percentage females) of fish among those that were sex-assigned and successfully aged was 56% (n = 291) in 2005 and 57% (n = 468) in 2006, and increased with river entry date

Fig. 2. Logistic regression of sex by marine exit date ($n = 759$, $p < 0.0001$). Circles represent individual fish and their respective sex from 2005 and 2006 samples. Lines (solid = predicted, dotted = $\pm 95\%$ confidence interval) denote the probability that a fish is female on a given marine exit date.

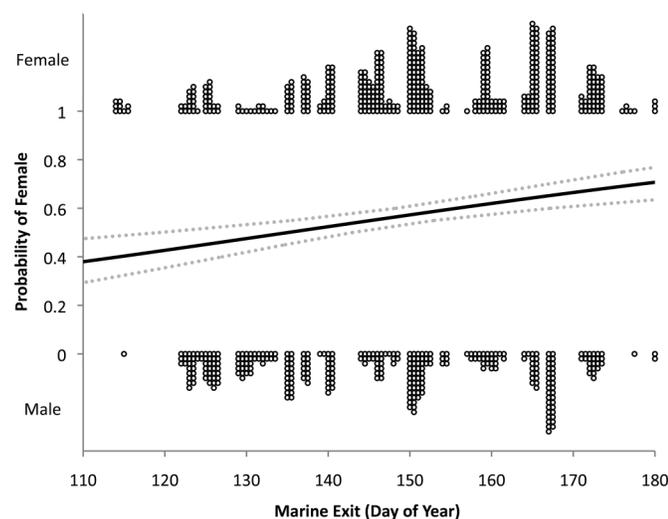
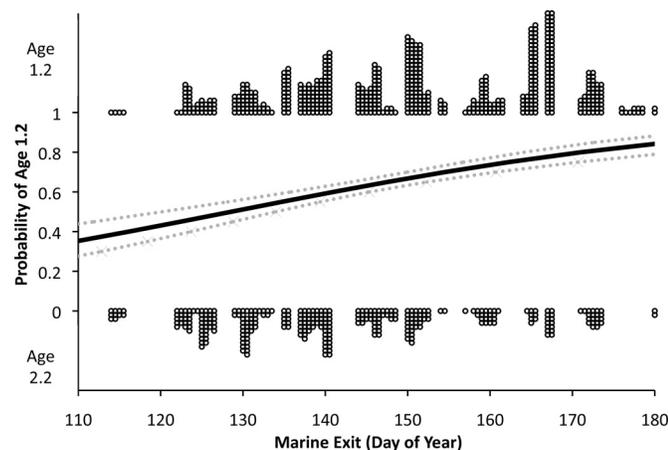
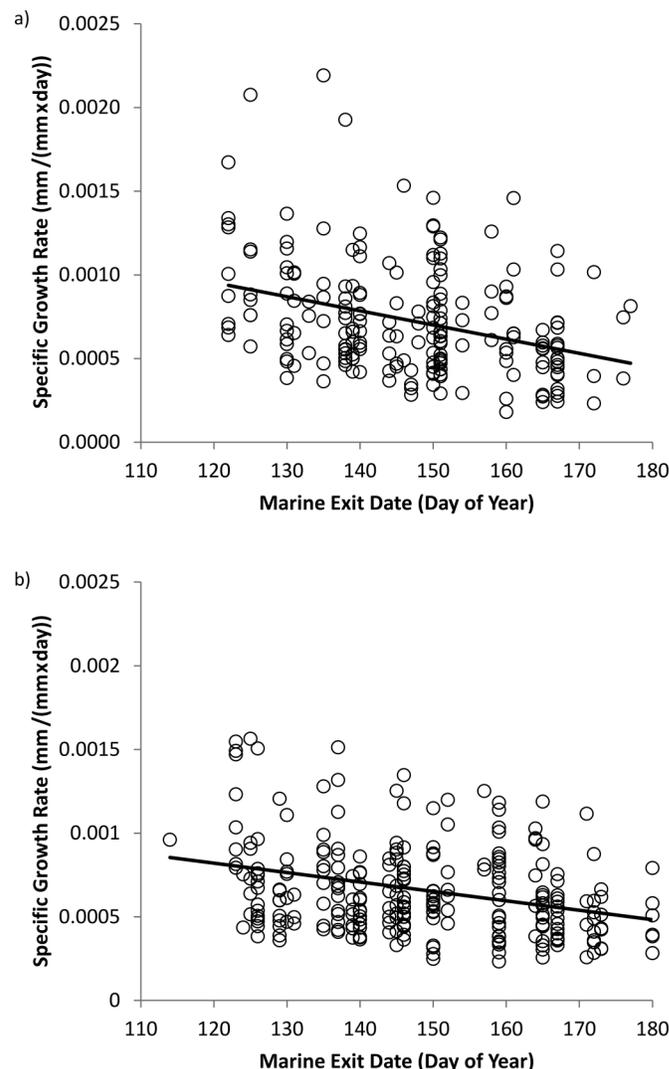


Fig. 3. Logistic regression of age class by marine exit date ($n = 882$, $p < 0.0001$). Circles represent individual fish and their respective age from 2005 and 2006 samples. Lines (solid = predicted, dotted = $\pm 95\%$ confidence interval) denote the probability that a fish is age 1.2 on a given marine exit date.



(logistic regression; $n = 759$, $p < 0.0001$; years pooled as no year difference detected; see Fig. 2). While the accuracy of sex allocations was not specifically tested, the data suggest that any error in sex allocations did not bias the results. The observed sex ratio was similar between fish that were assigned a sex based on external characteristics (56.8% female, $n = 563$) and fish that were dissected (56.6% female, $n = 196$). Furthermore, the overall sex ratio (percentage females) observed in dissected fish increased with river entry date (logistic regression; $n = 196$, $p = 0.0075$) similar to the larger data set that included fish with assigned sexes. The age class ratios (proportion 1.2 age class fish) were also near-identical in the 2 years (2005 – 65%, $n = 399$; 2006 – 63%, $n = 483$), and the proportion of 1.2 aged fish increased with river entry date (logistic regression; $n = 882$, $p < 0.0001$; years pooled as no year difference detected; see Fig. 3). Compared with 2.2 aged fish, the median exit date of 1.2 aged fish was 10 days later in 2005 and 6 days later in 2006 ($n = 399$, $p < 0.0001$ in 2005; $n = 483$, $p = 0.0004$ in 2006).

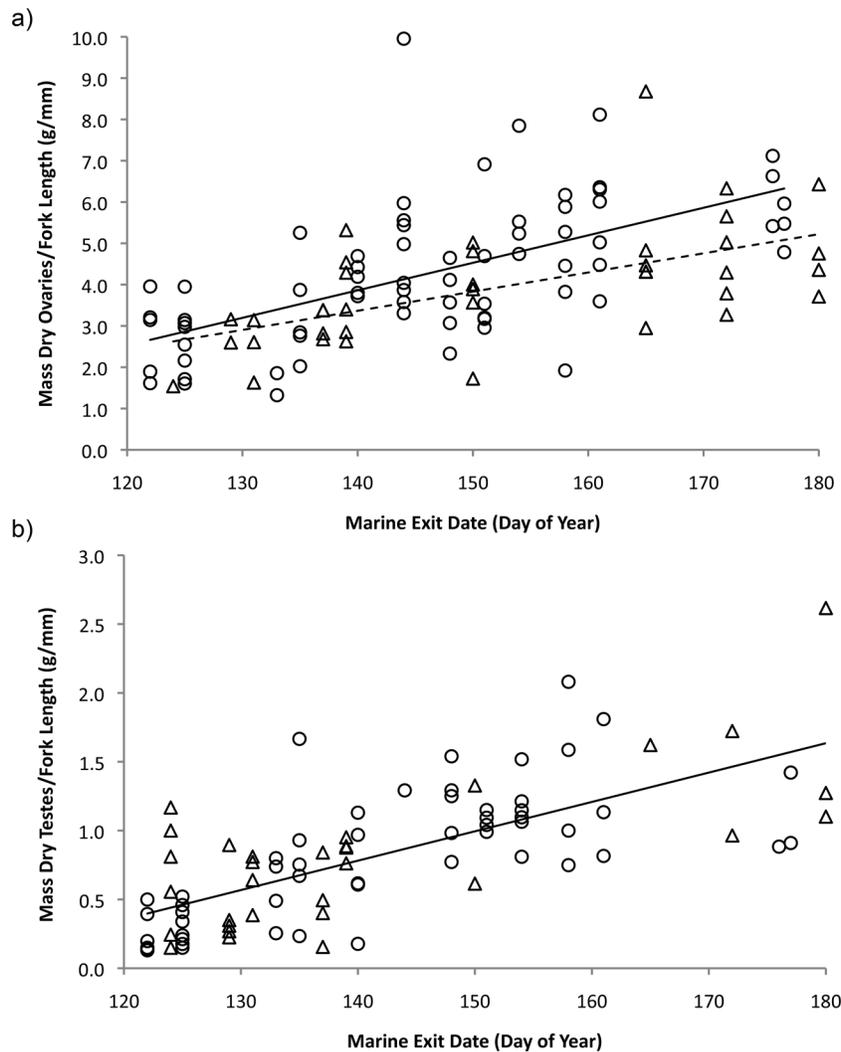
Fig. 4. Growth rates in spring prior to marine exit for sockeye salmon returning in (a) 2005 (two-factor regression: $r^2 = 0.17$, $n = 204$, date $p < 0.0001$, age $p = 0.0063$) and (b) 2006 (2-factor regression: $r^2 = 0.13$, $n = 263$, date $p < 0.0001$, age $p = 0.0013$).



River entry date was not correlated with growth during the first 2 years at sea (2005: $n = 204$, first year at sea $p = 0.04$; second year at sea $p = 0.35$; 2006: $n = 263$, first year at sea $p = 0.07$; second year at sea $p = 0.54$). But in both years, growth rate during the spring prior to river entry had a strong and significant negative relation with river entry date (Fig. 4). In estimating growth rate, scale samples that had signs of resorption (code > 2) were removed from the analysis, resulting in the rejection of 192 (44%) and 214 (48%) in 2005 and 2006, respectively. The probability of rejection was not correlated with river entry date (logistic regression; 2005: $n = 399$, $p = 0.44$; 2006: $n = 483$, $p = 0.18$), so there is no indication that the back-calculations of fork length and growth rates were biased.

In addition to sex, age, and growth rate, the body condition of sockeye salmon varied systematically with river entry date (Fig. 5) in a manner highly consistent between years. The dry mass of ovaries ($n = 68$, $r^2 = 0.39$, $p < 0.0001$ in 2005; $n = 38$, $r^2 = 0.37$, $p < 0.0001$ in 2006) and of testes ($n = 85$, $r^2 = 0.49$, $p < 0.0001$) both increased with river entry date. In ovaries, the dry mass of individual eggs increased by 5% per day ($n = 68$, $r^2 = 0.39$, $p < 0.0001$ in 2005; $n = 38$, $r^2 = 0.54$, $p < 0.0001$ in 2006), while fecundity

Fig. 5. Gonad size observed on a marine exit date. (a) Mass of dry ovaries/fork length at marine exit for fish returning in 2005, represented by circles and solid line ($n = 68$, $r^2 = 0.39$, $p < 0.0001$), and 2006, represented by triangles and the dashed line ($n = 38$, $r^2 = 0.37$, $p < 0.0001$). (b) Mass of dry testes/fork length at marine exit for fish returning in 2005, represented by circles, and 2006, represented by triangles ($n = 85$, $r^2 = 0.49$, $p < 0.0001$). Data for testes was pooled between years as differences were not detected between years.



decreased (Fig. 6) by approximately 25% between 1 May and 30 June (2005: $n = 68$, $r^2 = 0.11$, $p = 0.0069$; 2006: $n = 38$, $r^2 = 0.29$, $p = 0.0005$).

Comparisons of tissue composition between dorsal cross sections and complete carcasses ($n = 18$) were made in 2006. There were positive correlations between the dorsal cross sections and the complete carcasses in energy density (slope = 1.06, $r = 0.71$), lipid content (slope = 0.78, $r = 0.39$), and carbon content (slope = 0.82, $r = 0.63$), but not in protein content (slope = 0.005, $r = 0.00$). Cross sections had, on average, slightly lower mean energy density values (8.27 versus 8.81 MJ·kg⁻¹; $p < 0.0001$). Dorsal cross sections were, therefore, considered good indicators of total body energy density, carbon and lipid content, but not of protein content.

The energetic density of dorsal sections was negatively correlated with river entry date, declining at 0.010 MJ·kg⁻¹·day⁻¹ in 2005 ($n = 47$, $r^2 = 0.16$, $p < 0.01$) and 0.026 MJ·kg⁻¹·day⁻¹ in 2006 ($n = 89$, $r^2 = 0.46$, $p < 0.001$). The seasonal variation is driven primarily by variation in lipid concentration, which also decreased with river entry date (Fig. 7; $n = 47$, $r = 0.46$, $p = 0.0012$ in 2005; $n = 89$, $r = 0.57$, $p < 0.0001$ in 2006). Seasonal changes in the protein and carbon contents were small and inconsistent between years.

Discussion

Our results show that a set of individual traits is correlated with the river entry date of Copper River sockeye (Fig. 8). Earlier exiting individuals from the marine environment are more likely male, are more likely older (2.2 versus 1.2 age class), have a higher specific growth rate in the months prior to river entry, have greater somatic energy density, have smaller gonads, and (if female) have a larger number of (smaller) eggs. Despite ample variation, body size was not correlated with river entry date. Previous studies of salmonids (Burgner 1991; Kadri et al. 1995; Morbey 2000; Molyneux and Folletti 2005; Yamamoto and Edo 2006; Newell et al. 2007; Brodersen et al. 2008; Cooke et al. 2008) also report seasonal changes in one or more of these attributes, although we note that, in some cases, these the correlations are weak, albeit significant. Newell et al. (2007), for example, found significant but weak trends in age composition, size at age, and sex ratio for some Lake Washington sockeye populations that generally match those described here. We examine the marginal fitness benefits of the correlation of river entry timing to the set of individual traits.

Cooke et al. (2008) found that physiological measures of osmoregulatory preparedness provided little insight into migration

Fig. 6. Fecundity by marine exit date for females returning in 2005 ($n = 68$, $r^2 = 0.11$, $p = 0.0069$), represented by circles and solid line; and in 2006 ($n = 38$, $r^2 = 0.29$, $p = 0.0005$), represented by triangles and dashed line.

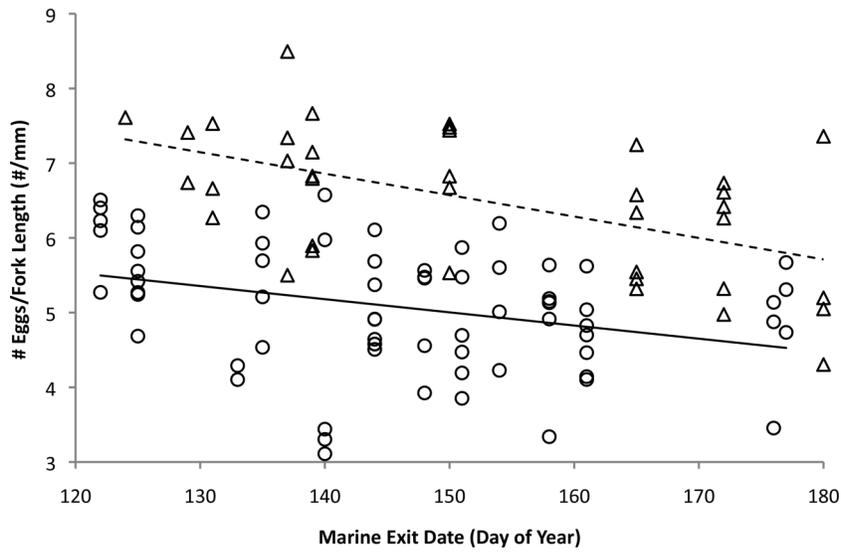
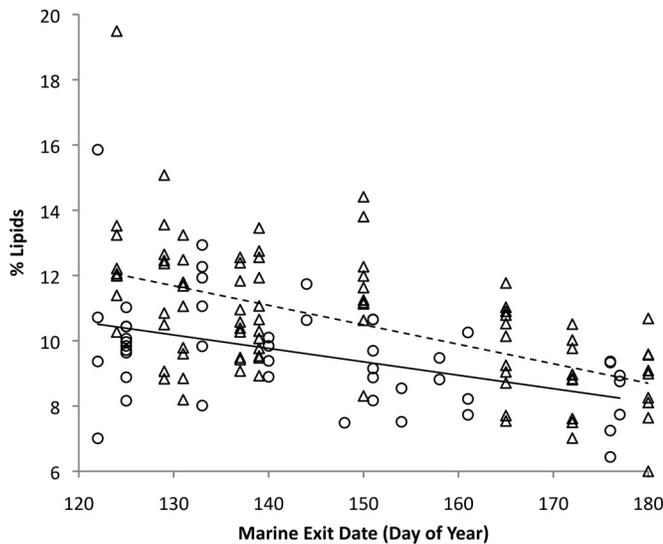


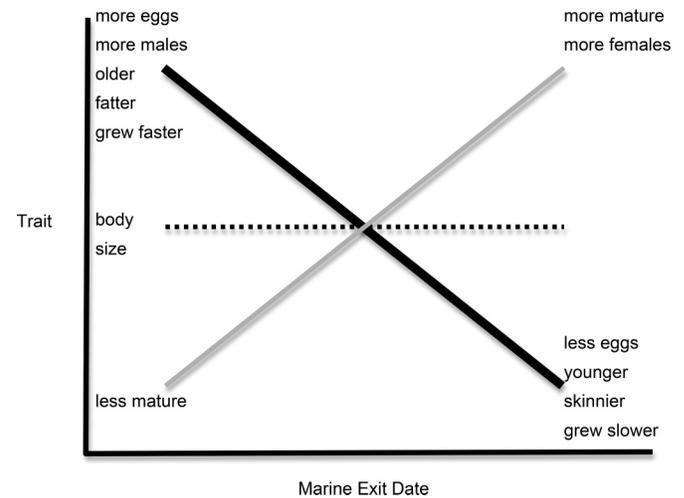
Fig. 7. Energy density as proportion of lipids in tissues by marine exit date of fish collected in 2005 ($n = 47$, $r^2 = 0.21$, $p = 0.0012$), represented by circles and solid line, and in 2006 ($n = 89$, $r^2 = 0.33$, $p < 0.0001$), represented by triangles and the dashed line.



timing of Fraser River sockeye. Seeking to understand the proximate factors associated with abnormally early migration timing of late-run sockeye salmon, they suggested that triggers for the earlier migration are associated with advanced reproductive development and higher energetic status. Others (Morbey 2000; Morbey and Ydenberg 2003; Yamamoto and Edo 2006) have considered the fitness costs and benefits of body size, condition, and timing of life history events. Brodersen et al. (2008), for example, suggested that lake-dwelling roach (*Rutilus rutilus*) trade off safety from predation and access to food differently depending on their body condition, which results in a condition-dependent partial migration. They concluded that each roach decides when to migrate (from the lake into a stream for breeding), based on an assessment of its own condition.

Copper River sockeye are small by comparison with other populations, as expected on the basis of the known correlation of body size with stream size (Beacham and Murray 1987; Lewis 1987; Quinn 2005). This correlation likely reflects the trade-off between

Fig. 8. Conceptual graph of findings regarding body condition metrics and marine exit date of Copper Creek sockeye salmon.



the higher reproductive benefits (Burgner 1991) and higher predation costs (Ruggerone et al. 2000; Quinn et al. 2003) associated with larger body size, with the costs weighing more heavily in smaller streams (Quinn et al. 2001). The lack of a seasonal trend in body size, also observed in other sockeye populations, implies that there is a cost to being large, but it is not clear whether this would be imposed during migration up the Copper River, during spawning in the three small tributaries of Skidegate Lake, or in both.

Strong and contrasting seasonal patterns may additionally constrain the development of a seasonal change in body size at river entry. The Alaskan Gyre (the region of the Pacific Ocean where sockeye feed) shows a seasonal cycle in zooplankton density (Brodeur et al. 1996), the peak of which corresponds to the median exit date of Copper River sockeye (see Fig. 1 in Katinić et al. 2015). Presumably, the growth rate attainable at sea follows this pattern, so that later-exiting individuals have slower growth in the weeks prior to exit. At the same time, the earliest exiting Copper River sockeye face a much longer period of freshwater residence prior to spawning (163 days) than the latest individuals (83 days), with a corresponding impact on the energy requirement. Katinić et al.

(2015) estimated that 1.5 kg females exiting on 5 May, 22 May, and 15 June, require 5382 kJ, 4805 kJ, and 4000 kJ, respectively, for maintenance metabolism. Accordingly, the allocation of reserves between maintenance and gonads differs strongly between early- and late-exiting individuals, with early-exiting fish having to allocate a much larger portion of each unit of gain for maintenance through the pre-spawning residence in Skidegate Lake. This complex of opposing tendencies may help explain why the condition-dependent exit patterns that we documented did not lead to a seasonal pattern in body size, and likely underlies the patterns we observed in gonad size and energy density.

Morbey (2000; see also Morbey and Ydenberg 2001) explained protandry in salmon by the “mate opportunity” hypothesis, under which males are under selection to arrive earlier than females to maximize their mating opportunities. Crossin et al. (2009) suggested that protandrous migration of Fraser sockeye salmon was a response by males to females who are under greater maturational constraints with respect to energy, reproductive development, and subsequent reproductive behaviour. However, due to the very long freshwater residence period prior to spawning, neither of these hypotheses is likely to apply to Copper River sockeye. Indeed, Katinić et al. (2015) found that early-exiting fish did not spawn earlier.

We propose that the earlier exit of males arises because the total energy cost of reproduction (gonad development plus reproductive behaviours) is lower for males than for females (Hendry and Berg 1999). Males can, therefore, allocate more resources to growth and energy reserves, with the result that, on any date at sea, they are slightly closer to their optimal size compared with females, which reduces the marginal fitness benefit of delaying river entry. Analogous reasoning is used to explain the differing river entry observed between 1.2 and 2.2 age classes. In this case, the two age classes experience the same growth opportunities at sea, but experienced different freshwater growth periods such that age 2.2 individuals migrated to sea approximately 10%–20% larger than their younger (age 1.2) cohorts (Katinić 2009). This size advantage persists through most of their lifetime and they reach the optimal size and energetic state required for reproduction prior to the 1.2 age class. The marginal fitness benefit of delaying river entry is, therefore, expected to be less for older fish.

In summary, intraspecific variation in the morphology of Copper River sockeye salmon appears to arise from a suite of condition-dependent life history tactics, under which females and age class 1.1 individuals delay river entry due to their slightly higher marginal fitness benefits (relative to males and age 2.2 individuals). While this research requires replication in other populations to examine the condition dependence of river entry more thoroughly, it demonstrates that sockeye populations that experience long delays between river entry and spawning are likely good candidate systems as they are less likely to be confounded by the behavioural strategies associated with spawning.

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